VOCALISATION RATES OF MIGRATING HUMPBACK WHALES OVER 14 YEARS

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Acoustic monitoring of migrating humpback whales has been carried out since 1981 in conjunction with visual surveys from Point Lookout, Stradbroke Island, on the east coast of Australia. Recordings were made from a drifting boat a few kilometres seaward of the observation point, during the peak of at least one of the annual migration phases. This paper presents an analysis of song vocalisation in relation to the observed movements of the whales to determine the vocalisation rates and their value as an index of relative abundance. The proportion of whales singing as they passed Point Lookout was ~5% during the northern migration (towards the breeding grounds) and ~13% during the southern migration, the difference being statistically significant. There was no significant trend in the proportion of singers as the stock size increased by a factor of 3. From 1982 to 1993, the number of singers passing per 10 hours during the southern migration increased at a rate of 10.6% (95% confidence interval 3% - 19%), consistent with the rate of increase of 11.7% obtained from the visual survey over a similar period. ❒ *Humpback whales, Megaptera novaeangliae, eastern Australia, vocalisations, song, stock recovery.*

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Sounds of humpback whales, *Megaptera novaeangliae*, have been recorded in the vicinity of Point Lookout on North Stradbroke Island on the east coast of Australia since 1981, usually at the same time as visual observations which have been made there regularly since 1978. This paper compares the acoustic and visual observations from 1981 to 1994. During that period, it is estimated that the number of humpback whales passing Point Lookout increased from ~600 in 1981 to ~2,300 in 1994, based on the stock size estimates and rates of increase from visual observations (Paterson & Paterson, 1989; Paterson et al., 1994).

Point Lookout is particularly suitable for visual observations. Humpback whales passing Point Lookout form the east Australian component of the Area V (130°E - 170°W) population which migrates annually between summer feeding grounds in Antarctic waters and winter breeding grounds inside the Great Barrier Reef (Chittleborough, 1965; Dawbin, 1966). The migration paths converge where the coast extends most eastwards, in the vicinity of Stradbroke I. and Cape Byron. Aerial surveys out to 80km from shore have shown that >95% of humpback whales pass within 10km of Point Lookout, and thus would be within visual range (Bryden, 1985). There have been land-based visual surveys from Point Lookout (Bryden et al., 1990; Paterson & Paterson, 1984, 1989; Paterson et al., 1994, 2001) and stock parameters and characteristics of the migration are well known.

Humpback whales are particularly vocal, producing both the well known song and 'social sounds' (Payne & McVay, 1971; Winn et al., 1971; Winn & Winn, 1978). The song appears to be related to breeding, possibly as an acoustic display, since the evidence is that singers are males and singing is usually confined to breeding grounds and migration paths to and from these grounds (Payne & McVay, 1971; Winn et al., 1971, 1973; Winn & Winn, 1978; Glockner, 1983; Cato, 1991). A song is a complex and well structured, but stereotyped sequence of themes and phrases of variable duration, but typically averaging ~10 minutes. Individuals may sing for several hours at a time and with the more powerful parts of the song audible for some tens of kilometres in most conditions (Cato, 1991).

This paper presents an estimate of the proportion of whales singing as they passed during migrations, which is of interest in understanding the function of the song, and in using acoustics to estimate abundance. It also tests the effectiveness of an acoustic index as an indicator of relative abundance by estimating the rate of increase of the stock from the numbers of singers passing per 10h in each year's observation period and comparing this with the result determined from visual observations.

MATERIALS AND METHODS

ACOUSTIC OBSERVATIONS. These were made using hydrophones suspended from a 4.5m boat, drifting off Point Lookout (Fig. 1). The hydrophone used from 1981 to 1983 was a General Instrument Corporation Z3B on 30m of cable, RAN Research Laboratory designed low noise preamplifiers and a Kudelski Nagra III tape recorder. System response was ± 3dB from 20Hz to 17kHz, but it was often necessary to use a high pass filter (-6dB at 55Hz, -20dB at 20Hz) to attenuate the low frequency noise from turbulence. From 1984, Clevite CH17 hydrophones and Sony WMD6 or TCD5M cassette recorders were used, giving a system response from 30Hz to 15kHz, modified by the above filter response when used.

During recordings, the boat was allowed to drift with the current to reduce the noise of turbulence from water flow past the hydrophone. The period of recording was chosen to coincide with the migration peak (late June, early July northbound and late September, early October, southbound) based on the rise and fall of numbers of humpback whales sighted in the region (Chittleborough, 1965; Paterson & Paterson, 1984, 1989; Paterson et al., 1994). Weather conditions were suitable for recording from a small boat on only about half the days over the one to two week observation period. There were two limitations. One was the difficulty of handling the boat in higher sea states and keeping the recording equipment dry and operational. The other was that higher wind speeds substantially increased background noise and substantially reduced distances that singers were audible. This limited effective recording to wind speeds of <20 knots. Limitations on opportunities to record at sea, and the small stock size in the earlier years limited the size of the sample, particularly the number of singers.

Bryden (1985) reported the distribution of humpback whales in the vicinity of Stradbroke I. based on aerial surveys from shore to 70km seaward of Point Lookout. He found that >95% of whales passed within 10km of the headland and >70% within 5km. Generally the position of the boat was within this 5km wide east west strip. Water depths where most whales pass Point Lookout increased with distance seaward from 20-90m and the boat was usually in depths of 30-50m.

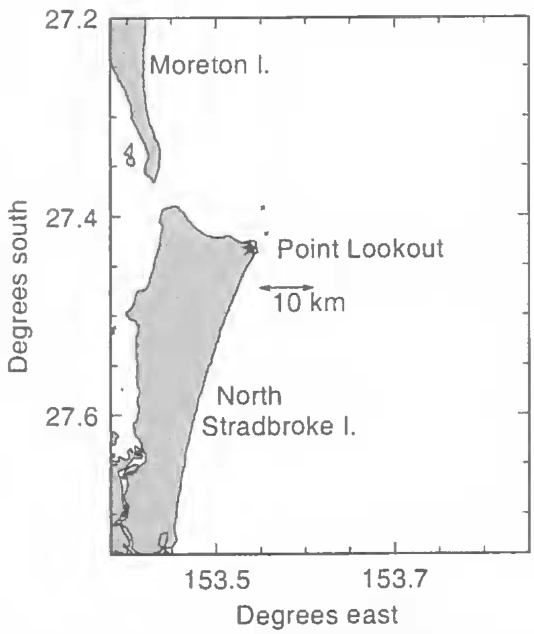

FIG. 1. Map showing the location of visual observation position on Point Lookout. Acoustic observations were made from a boat drifting a few kilometres seaward.

Analysis of the received sound signal levels and system calibration were made using a Brüel and Kjær Digital Frequency Analyser type 2131 and Hewlett- Packard 3582A analyser.

VISUAL OBSERVATIONS. These were made each year from the same 67m high position at Point Lookout (Fig. 1) and the methods conformed with surveys dating from 1978, described by Paterson et al. (1994). A continuous watch was maintained during daylight for each day of the observation period in the earlier years of this study, and on three to four days per week over a longer period during the later years. Visual observation covered a larger part of the migration period than the acoustic observations. While we attempted to ensure that visual and acoustic observations were concurrent, this was not always possible. The area of ocean within visible range covered a sector between true bearings of 030° and 120° and extending to about 10km from shore under typical conditions. The boat was allowed to drift within this sector and was usually 3-5km seaward of the headland, though on some occasions it was out of sight. Humpback whales passing through the sector were usually seen a number of times and depending on their positions, paths taken and sighting conditions were

TABLE 1. Summary of the data.

	Northern migration	Southern migration
Years of acoustic data	1984, 1989-91, 1994	1981-89, 1992, 1993
Years of concurrent acoustic and visual data	1984, 1989-91, 1994	1981-85, 1987, 1991, 1992
No. of days acoustic data Total all years Yearly range, average	 26 3 - 7, 5.2	 44 2 - 5, 4.0
No. of hours acoustic data Total all years Yearly range, average	 145.9 18.0 - 46.1, 29.2	 247.4 10.1 - 36.7, 22.5
No. of hours of concurrent acoustic and visual observations	118.9	159.9

visible for <1h to >5h. Table 1 summarises the data for all acoustic observations and for those taken concurrently with visual observations.

BASIS FOR THE ACOUSTICS ANALYSIS

THE EFFECT OF THE OCEAN ENVIRONMENT ON AUDIBILITY OF SINGERS. The distance over which a source in the ocean is audible (by ear) or detectable (by instrumentation) varies widely because of variation in ocean conditions. The limiting range of detection depends on the source level (power generated by the source), the propagation loss as sound travels to the receiver, and the background noise against which the signal must be detected. The received sound signal will be detected or heard if the signal to noise ratio exceeds a certain threshold value.

Sound travels to much greater distances in the ocean than it does in the atmosphere because the absorption attenuation, the loss of energy from the sound wave, is much lower. Propagation in shallow water (<200m) involves many reflections from the sea surface and the bottom. While surface reflection occurs with little loss, reflection from the bottom may involve significant energy loss which varies widely for different bottom materials. Consequently propagation loss varies widely from one shallow water site to another. Temporal variability depends on variation in the sound speed-depth profile and this depends on the mixing of the water by surface waves and currents. Surface wave action tends to mix the water and minimise this variability, as was the case in the study area where significant wind and wave action is usual. The variability of propagation loss can be minimised in shallow water by confining the work to a fixed location, as in this study. Shoals and reefs tend to block the propagation of sound and need to be avoided and we usually positioned the boat to have clear path to passing whales.

There is a general ambient or background noise in the ocean due to contributions from many physical and biological sources of sound. The good propagation of sound allows contributions from sources at much greater distances than in the atmosphere so the noise level is high and variable. Ambient noise in Australian coastal waters varies by more than 20dB mainly as a result of variations in wind speed and biological activity (Cato, 1997). Breaking waves generate high noise levels which are directly related to wind speed (and less to the actual wave height or sea state, Wenz, 1962). Fish and invertebrates, such as snapping shrimps (Everest et al., 1948) also produce high noise levels, which vary temporally with diurnal and other variations in behaviour, and spatially with habitat variation (McCauley & Cato, 2000). The effect of an increase of 20dB in ambient noise is to reduce the amount of propagation loss that can be tolerated at the threshold of detection by 20dB. In free field propagation, this corresponds to a factor of 10 in distance, more if the sea floor is highly reflective or less if it is highly absorptive. Consequently the typical variation of ambient noise in coastal waters causes the distance of audibility to vary by a factor of ~10. The consequent variation in the area over which singers are audible would be a factor of ~100, since the area depends on the square of the distance. Thus simply counting the number of singers audible is of little value in estimating stock parameters, unless the effects of ambient noise and sound propagation are accounted for.

The effect of ambient noise can be removed by measuring the level of the received signal, since this equals the difference between source level and propagation loss, and is thus independent of ambient noise. This requires the received signal to noise ratio to be above the threshold of detection, but the high source levels of whale sounds means that this would normally be the case for sources at distances of kilometres to tens of kilometres. If the source level and propagation loss are known, the distance to each source can be calculated.

Our perception of the loudness of a sound received underwater is of almost no value in estimating the received level, since this depends on the signal to noise ratio. We hear the sounds through headphones or a loudspeaker so our only criterion for judging the loudness of the signal in absolute terms is to compare it with the background noise. The wide variation in ambient noise causes wide variation in apparent loudness, and for the same loudness, singer distances vary as ambient noise varies. This may be counter intuitive but results because the decrease in received signal level with distance in the ocean, even to distances of tens of kilometres, is far more gradual than the decrease with distance in air. A doubling of the distance results in only a small change in received level, much smaller than the variation of ambient noise.

APPLICATION OF ACOUSTICS TO STOCK ASSESSMENT. An estimate of the abundance of a whale stock usually involves sampling the spatial or temporal density of individuals and scaling the results up to the full spatial or temporal extent of the stock. For example, for a stock that is resident in an area, samples of the spatial density are made and the result then scaled up to the total area. Off east Australia the stock is migrating and as most whales pass within visual range of headlands such as Point Lookout, the approach has been to sample the temporal density by counting the number of whales passing per 10-h day on the basis that any individual would pass through the area only once in a migration. The result is then scaled up to the total period of migration (see for example, Bryden et al., 1990; Paterson et al., 1994).

The use of acoustic observations to determine spatial densities requires an estimate of the distances to singers so that only those within the area of the sample unit are counted. In temporal sampling, it is also necessary to estimate the distances of singers to ensure that they are close enough to pass the observation point within the sampling period, since singers may be audible for tens of kilometres. The most accurate way of determining distances is to use an array of three or more accurately positioned hydrophones, which also allows sources to be localised and their movements tracked from the differences in times of arrival of signals to the different hydrophones. Some examples of this method applied to locate baleen whales are given by Cummings & Holliday (1985) and Clark, Ellison & Beeman (1986) for bowhead whales, *Balaena mysticetus*, and Frankel et al. (1995) for humpback whales (see Noad & Cato, 2001, for further discussion and application to the east Australian humpback whale migration). This method is logistically complicated and requires substantial analysis effort.

Simpler methods of estimating distances may be more attractive for routine surveys because of lower cost and effort, but are less accurate and will result in greater errors through variability in source levels and propagation loss. Little data on variation of source levels of baleen whale sounds area available, though significant variation has been observed for bowhead whales (Cummings & Holliday, 1987) and finback whales, *Balaenoptera physalus*, (Watkins et al., 1987).

In the present study, determination of the proportion of passing humpback whales that were singing was made by comparing the concurrent acoustic and visual observations. If a singer was audible, it was necessary to establish that it was one of the whales seen passing and not a more distant whale. This was done by measuring the received level of the sounds and estimating the distance of the source based on estimates of source level and propagation loss. In many cases it was not possible to identify the particular whale that was singing because of the uncertainties of the estimate, but it was possible to establish that the singer was among the visually-observed passing whales. Only the most intense sounds of the song, usually low frequency moan-like sounds were used to determine if a singer was one of the visually observed whales. These sounds are considered to be the most consistent for this purpose, in that they tend to persist with less yearly change and they also provide the best signal to noise ratios.

Where the singer could be identified unambiguously, it was possible to make an estimate of the source levels of the sounds. Propagation loss was estimated using the semi-empirical expressions of Marsh & Schulkin (1962) for shallow water. At the short distances at which these estimates were made (usually within 300 m, a few times the water depth) this should be reliable. Measured broad band mean square source levels varied from 176-185dB re 1μPa at 1m. Some of the variation is due to variation between the different sound types but there would be a significant uncertainty due to errors in estimating the distance to the source (which was done by eye). The results are, however, consistent with the range of 175-188dB re 1μPa at 1m reported by Winn et al. (1971) and the mean measured in a 300Hz band by Frankel (1994) of 174dB re 1μPa.

From the received level, an estimate was made of the range of possible distances of a singer given the variation in source level and uncertainty in propagation loss. This was then compared with the positions of whales observed visually.

Singers were usually audible for several song cycles, often for more than an hour, allowing a number of different estimates as positions of the whales and singer changed. When the singer was closest, the uncertainty in its position was least.

A different approach was used in determining an index of relative abundance to test the effectiveness of acoustics in estimating the annual rate of change of stock size. Since this has potential application for situations where there are no visual observations, there was an advantage in developing an index that was independent of visual observations. The index chosen was a count of the number of singers passing per 10h listening, averaged over the total listening period for each year. The criterion used to establish that a singer heard was passing was that it passed within 5km of the boat, based on the received level of the sounds, the propagation loss and source level. This covered a 10km-diameter circle centred on the boat drifting a few kilometres from shore, and was chosen to match approximately the 10km wide strip of the visual observations. An error in the estimate of propagation loss would change the size of this circle, but since this would be consistent from year to year, the error would not affect the value of the criterion as a relative index of abundance. There remains some uncertainty due to possible variations in source level. Because singers were audible for long periods, minimum estimated distances were usually significantly <5km, reducing uncertainty in the results. All acoustic data were used in this analysis, irrespective of whether there were visual observations during the same period, while the estimate of the proportion of whales singing was confined to data that were concurrent with the visual observations.

RESULTS

PROPORTION OF HUMPBACK WHALES SINGING. Table 2 compares the total numbers of singers passing with the total numbers of humpback whales passing during the periods of concurrent acoustic and visual observations. An average of ~5% of passing whales were singing on the northern migration and 12% on the southern migration. A Chi squared test (Siegel & Castellan, 1988) showed that the difference in the results for the two migrations was significant ($P < 0.05$). Figure 2 shows results for the southern migration as a plot of the number of singers in each year versus the number of whales passing. There is a good correlation between numbers of singers and total numbers of whales passing (correlation coefficient 0.989) and the slope of the linear regression line on the data provides another measure of the proportion of whales singing. The slope of 0.132 (95% confidence interval 0.105-0.160 %), gives a value of 13.2% (± 2.8%) for the proportion of whales singing, consistent with the proportion obtained from the total numbers of singers and whales. The number of singers versus whales passing during the northern migration is shown in Fig. 3. The spread of data for the northern migration is too small to obtain meaningful regression of singers on total whales.

Tyack (1981) found that out of 129 humpback whales observed in the Hawaiian breeding grounds, 21 were singing, a proportion of 16.3%. A Chi square test (with correction for continuity) did not show a statistically significant difference

TABLE 2. Number of singers passing compared with total numbers of whales passing Point Lookout.

	Northern migration	Southern migration
Years of observations	1984, 1989-91, 1994	1981-85, 1987, 1992, 1993
Hours of observation	118.9h	156.7h
Singers passing, total	8	27
Singers passing when concurrent acoustic and visual observations	7	12
All whales passing, total	141	114
All whales passing when concurrent acoustic and visual observations	141	100
Proportion singing (range of results for each year) from totals	0.05 (0.028 - 0.083)	0.12 (0.083 - 0.130)

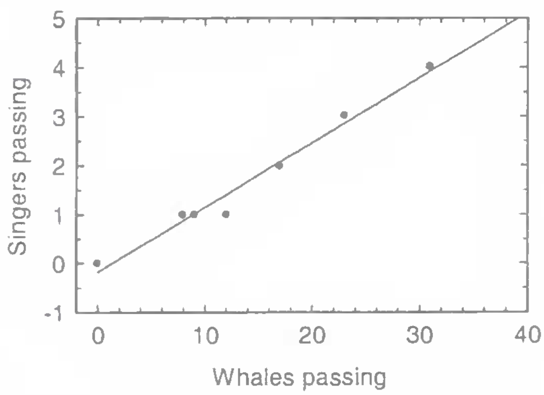

FIG. 2. Relationship between the number of singers and the total number of whales passing Point Lookout, at the peak of the southern migration each year (1982-1989, 1992).

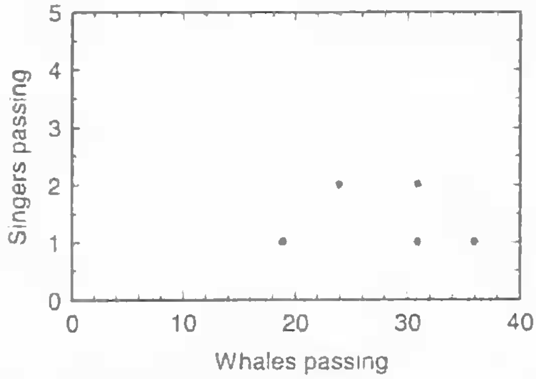

FIG. 3. Relationship between the number of singers and the total number of whales passing Point Lookout at the peak of the northern migration each year (1984, 1989, 1990, 1991, 1994).

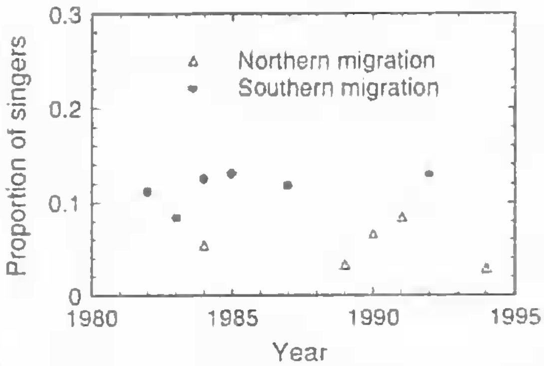

FIG. 4. Proportion of whales singing as they passed Point Lookout for each year of observation at the peaks of the northern and southern migrations.

between the Hawaiian result and the east Australian southern migration result ($P < 0.5$).

Figure 4 shows the year by year proportion of singers passing from 1982 to 1994. Little consistent trend with year is evident in the data for either migration, within the spread of the data.

ACOUSTIC INDEX OF RELATIVE ABUNDANCE. Figure 5 shows the average number of singers passing per 10h for each year of observations during the southern migration. A logarithmic scale is used for the number of singers so that a constant rate of increase (or exponential increase) would appear as a straight line. The results show an increase over the years, though there is significant spread of data. A linear regression line was calculated for the logarithm of singers per 10h versus the year of observation to obtain the best estimate of a constant rate of increase. This gave a rate of increase of 10.6% with a 95% confidence interval of 3.1-8.6% and correlation coefficient of 0.76. This result, for the period 1982 to 1993 is consistent with the rate of increase of 11.7% (95% confidence interval 9.6-13.8%) obtained from visual observations from Point Lookout from 1984 to 1992 (Paterson et al., 1994), though the confidence interval is much wider for the acoustic result. The acoustic observation sample represent a much smaller number of individuals, partly because only a proportion of the passing whales was singing and partly because of the shorter period of observation in the acoustic survey. The number of singers in a year varied from 1 to 6 so the spread in the data in Fig. 5 is to be expected, and such a small number of individuals limits the reliability of the sample.

In an attempt to improve the sample size, numbers of singers per 10h were pooled in two year blocks and the results are shown in Fig. 6. The result shows less spread of data and the regression line gives a rate of increase of 12.4% with 95% confidence interval of 10.9-13.9%, within the range obtained from visual observations. This result suggests that a longer period of observation with the detection of more singers would have been appropriate for the purpose of estimating relative abundance.

Data for the northern migration were considered insufficient to obtain a reliable estimate of the rate of increase in stock size, with fewer years and smaller proportion of singers than for the southern migration.

DISCUSSION

Although sample sizes were small when measured in terms of the numbers of singers passing Point Lookout, the results do show consistency.

Humpback whale singing is considered to be related to breeding. It is usually observed on the breeding grounds and on migration to and from the breeding grounds (Payne & McVay, 1971; Winn et al., 1971; Winn & Winn, 1978; Cato, 1991), but is rare in higher latitudes where most feeding occurs. While the proportion of whales singing on the southern migration off Stradbroke I. is significantly higher than that for the northern migration, it is consistent with that observed on the Hawaiian breeding grounds. There is no apparent environmental difference off Point Lookout between the two migrations. Monthly averages of water temperatures differ by <1°C between the times of the two migrations

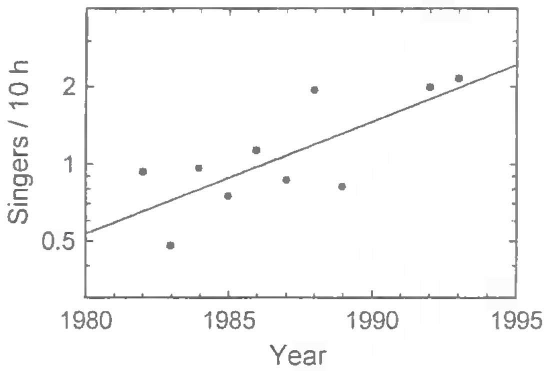

FIG. 5. Number of singers passing Point Lookout per 10h at the peak of the southern migration in each year of observation.

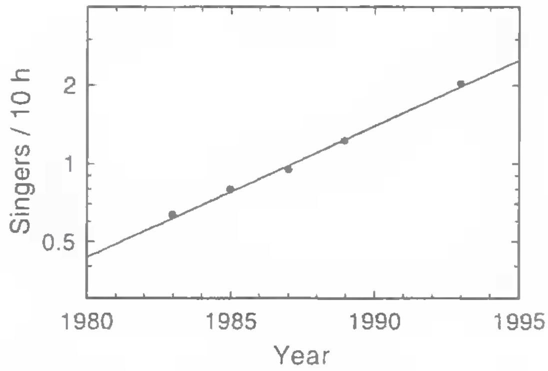

FIG. 6. Numbers of singers passing Point Lookout per 10h at the peak of the southern migration – data pooled in two-year blocks. Point shown for each year is the data pooled for that year and the previous year.

(Paterson, 1986), less than the variation observed in measurements from the boat within a migration period. While there is evidence that singing is confined to mature males (Winn et al., 1973; Glockner, 1983), the proportion of mature males passing at the times of recording is similar for the two migrations (Chittleborough, 1965; Dawbin, 1997). This suggests that the whales are closer to breeding condition on the southern migration, moving away from the breeding grounds than they are on the northern migration, when approaching the breeding grounds. Humpback whales are clearly in transit as they pass Point Lookout — whales pass through the observation area with relatively little deviation and only occasional significant interaction. The southern migration, however, shows more meandering and surface interaction than the northern migration, and if this is interpreted as behaviour indicative of the breeding areas, this is consistent with the increased proportion of whales singing during the southern migration. There is, however, greater similarity in behaviour between the two migrations, than there is between that on the southern migration and on the Hawaiian breeding grounds.

The humpback whale stock passing Point Lookout is estimated to have increased from ~600 in 1981 to ~2,300 in 1994 (Paterson & Paterson, 1989; Paterson et al., 1994). Over the period of the southern migration data it varied from ~660 in 1982 to ~2,100 in 1993, a factor of >3. The migration has remained consistent over this period, based on the lack of apparent change in its timing, the rate of rise and fall in numbers passing over the course of the migration and the consistency in the proportion of the stock passing in 4, 8 and 10 weeks at the peak in 1987, 1992 and 1999 (Paterson et al., 1994, 2001). Thus the spatial and temporal separation of the migrating humpback whales can be expected to be inversely proportional to the stock size, i.e. to have decreased by a factor of >3 from 1982 to 1993. In 1982, the average temporal separation between groups of whales passing during the four weeks at the peak of the southern migration would have been ~4.9h (based on an average group size of 2.17, Paterson et al., 2001) and the average separation of singers would have been ~17h. Using the estimates of migration speed of Dawbin (1966) (~1.5 knots for long-term movement of stock) and Chittleborough (1965) (mean of 3.4 knots from aerial observations), the average separation of groups would have been from 13.6-39km and the average separation of singers 47-136km. This raises the question of how changes in the song are communicated over large distances, given the separation of whales. In 1983 and 1984, songs recorded within a few weeks at locations separated by thousands of kilometres along the east coast of Australia were similar, even though the song was changing (Cato, 1991).

The lack of significant trend to a change in the proportion of whales singing over the period when the stock size increased by a factor of three, suggests that singing is not driven by the density or proximity of singers or non singers. In the early years of our observations it was very unusual to hear more than one singer at a time whereas in the later years, two or more were usually audible. Difference in the proportion of whales singing between the two migrations also suggests that singing is internally driven. In a captive female leopard seal, production of intense song-like sounds was highly correlated with hormonal changes related to breeding (Rogers et al., 1996). If production of song is driven by hormonal changes, this would be independent of the density and proximity of singers and non singers, and would also be consistent with a higher proportion of singers when behaviour is more indicative of breeding as on the southern migration.

These considerations also support the view that the humpback whale song is an acoustic display associated with breeding. The lack of dependence of song production on separation of singers and non singers suggests that the singing is not interactive or agonistic communication between individuals. Although the song is complex and contains a large number of sound units of different kinds, it is very stereotyped. Since information is carried only in variations in the stereotype (Cato, 1991), most of the potential to carry information is not used and this further supports the idea of the song as an elaborate acoustic display.

Extensive data concerning east Australian humpback whale population parameters have been obtained from long-term visual observations at Point Lookout. Stock size and rate of increase are well established. The similarity of the rate of increase in stock size estimated from the acoustic data to that estimated from visual observations, indicates that acoustics may be useful in estimating relative abundance with simple recording systems in areas where visual observations are more difficult to conduct effectively.

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